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Minimizing the chaos following the loss of Article 59: Suggestions for a discussion

Walter Gams[1], Richard A. Humber[2], Walter Jaklitsch[3], Roland Kirschner[4] & Marc Stadler[5^]

[1] *Molenweg 15, 3743CK Baarn, Netherlands*
[2] *USDA-ARS BioIPM Research, RW Holley Center for Agriculture & Health, 538 Tower Road, Ithaca, N. Y. 14853-2901, USA*
[3] *Department of Systematic and Evolutionary Botany, University of Vienna, Rennweg 14, A-1030 Vienna, Austria*
[4] *Department of Life Sciences, National Central University, No. 300, Jhongda Rd., Jhongli City, Taoyuan County 32001, Taiwan (R.O.C.)*
[5] *Helmholtz Institute of Infection Research (HZI), Dept Microbial Drugs, Braunschweig, Germany*
* Correspondence to: *walter.gams@online.nl*
^ (authors in alphabetic sequence)

Abstract — We assert that the suppression at the 2011 Melbourne Botanical Congress of the dual nomenclature for pleomorphic fungi was premature since most fungal genera still remain inadequately typified and need molecularly based revisions. The new system turns a rule-determined nomenclature into a system of names to be decided by committees. The new system cannot be implemented until experts publish well-documented rationales about the generic names to be accepted or suppressed among alternative morphs and the responsible committees act officially. Prioritization vs. suppression is not the same as conservation vs. rejection. If a teleomorphic generic name is suppressed, it still remains valid and legitimate and can still serve as a basis for names of higher-rank taxa. In most cases the teleomorph genus name should be prioritized unless convincing arguments favor preference of the anamorph name. Paraphyletic genera must be recognized. Unless the phylogenetic positions of all type species for possible morphs are confirmed, no prioritization can be fixed. When a binomial in a prioritized genus has a younger epithet than the corresponding name in the suppressed genus, only priority of extant names in the prioritized genus should count.

Key words — anamorph-teleomorph connection, competing morph names

Unification of fungal nomenclature (one name, whether teleomorphic or anamorphic, is allowed for each taxon) had to come eventually (Hawksworth et al. 2011, Norvell et al. 2011), but the move is being enforced much too early while only a minority of fungal taxa has been examined phylogenetically

(Hibbett et al. 2007). As currently circumscribed, too many fungal genera are unconfirmed as homogeneous and monophyletic (such proofs may not be possible for some genera), and knowledge of correlations between anamorph and teleomorph genera is far from comprehensive (Gams et al. 2011); however, Hawksworth et al. (2011) cited the ability to link anamorphs and their teleomorphs by molecular means as a key reason for the rapid adoption of the new rules. Names of lichenized fungi have always been excluded from dual nomenclature and are little affected by the issues discussed here (Lendemer 2011). While the previous Article 59 might not be reinstated (and cannot even be considered until the 2017 International Botanical Congress), we must find solutions to minimize the disruptive effects of this decision for fungal nomenclature and systematics. That the new procedures will depend on committee decisions listed in databases rather than on adherence to clear-cut rules of a Code will obviously be a source of conflicts.

A key sentence in Paragraph 1 of the Preamble in the ICBN (McNeill et al. 2006) is crucial to our argument: "This Code aims at the provision of a stable method of naming taxonomic groups, avoiding and rejecting the use of names which may cause error or ambiguity or throw science into confusion." This fundamental principle seems to be ignored by what has happened: Previous editions of the Code established democratically accepted rules subject to adjustment every six years by general voting in the Nomenclature Sessions. The newly prescribed rules and processes for determining the correct names for pleomorphic fungi reject these long understood, fair rules in favor of non-appealable decisions rendered by a series of Committees. It is still unknown how these newly adopted processes will be put into practice. Language adopted in Melbourne requests "consultation with" but does not actually mandate the involvement of non-IAPT committees (that have no legal standing vis-à-vis the Code). Nomenclatural stability, a principle long stated in the Code, seems to have been abandoned in favor of committee-based decisions governing the choices and applications of names for exactly those fungi whose complex biologies and multiple reproductive forms need governance by clear rules, not by consensus in committees.

Gene-based data can never be the sole basis for meaningful, informative classifications of any organism without also incorporating the essential foundations of morphology and other traditional characters. Imperfectly known taxa (new or old) need to be recollected for more study of their genes and morphologies before being reclassified. Fieldwork and ecological and morphological studies will be indispensible to the additions into GenBank of genetic data for innumerable neglected taxa. Deposits of accurate gene sequence data from incorrectly identified source organisms is a widespread problem that can confuse and seriously damage later analyses based on false assumptions.

While environmental DNA sampling might indicate that fungi are present, it reveals nothing about the appearance and biology of the fungi from which that DNA came, how to recognize them, or whether and how these fungi interact with any other organisms.

Some supporters of the one-fungus one-name (1F=1N) concept seem to assume that all fungi will readily yield good DNA and clean sequences. However, many entomophthoraleans resist repeated attempts by skilled technicians to obtain clean DNA and useful amplifications of genes now widely accepted (and expected) to provide phylogenetically informative data. Some taxa in the *Xylariaceae* yield either no cultures from too-scanty available materials or no useful PCR products from even freshly collected stromata. Further, some xylarioid stromata have at times provided contaminant DNA that was later shown to represent different taxa of the same or closely related xylariaceous genus (Stadler et al. 2010, Stadler 2011). Although *Xylariaceae* harbors few known endophytic species, some do grow hyperparasitically on xylarioid taxa; consequently, DNA extraction from stromata should be strongly discouraged, given that which organism provides the DNA sequence within a xylarioid stroma may remain uncertain. Endolichenic fungi may cause even more confusion (Arnold et al. 2009). As fungi generally grow in complex aggregations in nature, often only a skilled morphologist can ascertain that a culture actually represents what was thought to be the original inoculum. Some fungi may never be culturable unless new techniques are developed for isolation and growth, while special methods may also be needed to purify and to amplify their DNA. Anamorph-teleomorph relationships can hardly be proven in such cases, and phenotype-based taxonomic concepts MUST be maintained for the time being.

Implementation of the new rules

New paragraph approved in Melbourne:

> Art. 57.2 (**new**) In pleomorphic fungi (including lichenicolous fungi, but excluding lichen-forming fungi and those fungi traditionally associated with them taxonomically, e.g. *Mycocaliciaceae*), in cases where, prior to 1 January 2013, both teleomorph-typified and anamorph-typified names were widely used for a taxon, an anamorph-typified name that has priority **is not to be taken up** until retention of the teleomorph-typified name has been considered by the General Committee and rejected [OUR EMPHASIS].

This rule implies that the duality of names should not be suppressed until the responsible committees have rendered and publicized their decision about the preferential use of a particular name. Thus, mycological editors should be patient and tolerant with authors who may still prefer to use teleomorph-typified generic names, even if the corresponding anamorph name is older.

Prioritization—choosing between competing morph names for an individual pleomorphic fungus—vs. conservation.

New text passed in Melbourne to appear in the ICN:

> Art. 14.13 **(new)** In the interest of nomenclatural stability, for organisms treated as fungi (including lichenicolous fungi, but excluding lichen-forming fungi and those fungi traditionally associated with them taxonomically, e.g. *Mycocaliciaceae*), lists of names may be submitted to the General Committee, which will refer them to the Nomenclature Committee for Fungi (see Div. III) for examination by subcommittees established by that Committee in consultation with the General Committee and appropriate international bodies. Accepted names on these lists, which become Appendices of this Code once reviewed and approved by the Nomenclature Committee for Fungi and the General Committee, are to be listed with their types together with those competing synonyms (including sanctioned names) against which they are treated as conserved (see also Art. 56.3).

Prioritization. We strongly suggest referring to the choice among competing morph names as **prioritization,** an action that is not equivalent to conservation. While Art. 14.13 requires such choices to be "treated as conserved," such status would confer permanent validity to frequently misapplied names.

To clarify this, Art. 14.13 should be amended to deal with suppressed names. Among competing anamorphic (occasionally synanamorphic) and teleomorphic names for the same taxon, one of the "name pair" will be given preference while the use of the other(s) is suppressed. Although suppressed names are not available for use, however, they remain nomenclaturally valid and legitimate. This condition differs fundamentally from the status of a nomen rejiciendum. In contrast to conservation, an act of prioritization need not be irreversibly fixed if convincing arguments support a change.

Consequently, names of teleomorphic genera that may be suppressed in favor of associated anamorphic generic names remain available as bases for higher-rank names and would not disrupt the current general systematics of *Ascomycota* that would be severely affected by the issues discussed here.

Until July 31, 2011, teleomorph-typified names had **precedence** over anamorph-typified names irrespective of temporal priorities. Under the new rules, priority of publication should generally determine the choice. It is, however, true that the great majority of names for fungal families (and higher ranks) are based on teleomorph-typified genera. Because all teleotypified generic names remain legitimate and available as a basis for higher-rank taxon names, there is no objection to this (Art. 18.3 ICBN), and no changes at higher-rank names will become necessary for purely nomenclatural reasons. Basing any higher-rank names on anamorph-typified generic names might be desirable in some cases, but it must be discussed. If, for example, the name *Trichoderma*

were prioritized over *Hypocrea*, should this require introducing the names '*Trichodermataceae*,' '*Trichodermatales*,' etc.? Because family names adhere to the rule of priority, would the name '*Trichodermataceae*' have precedence over *Hypocreaceae* simply because of the priority of the genus name?

The new rule abandoning the preference of teleomorph-names for higher ranks of fungi may encourage the description of many higher taxa (families, orders, etc.) for clades of exclusively anamorphic *Ascomycota*. This would be a new — and undesirable — situation. Certain anamorph names have later been correlated with symplesiomorphic characters that have little or no use in formal taxonomy but do serve as descriptive terms.

For the prioritization of single or listed fungal names well-documented PROPOSALS must be submitted and published, e.g. in TAXON, as well as posted on an appropriate website. It might be helpful to first propose a **preliminary prioritization** that would become definitive only after a certain period of testing (e.g., after 2 years).

Decisions about prioritization will be made by **authorities** comprising a) a committee of experts (the largest, most diverse group reasonably possible), b) the International Committee for the Taxonomy of Fungi (ICTF), and c) the IBC Permanent Nomenclature Committee for Fungi (NCF). The NCF then will report to the General Committee. A majority of at least 60% of the votes (the NCF present practice—including abstentions, but suggested for (a) excluding abstentions) should be required for a decision. Art. 14.13 alludes to committees a) and b) as "appropriate international bodies." A primary concern is, who will bear the responsibility of establishing individual committees of experts?

The size and scope of any expert committee must vary according to the fungi under consideration to assure diverse points of view and geography; the constitution of these committees should and must be debated — and consensus reached — before they are established. The greatest problem will be finding mycologists competent in all fungal groups to be tackled. If enough experts are not found for a particular group or if no molecular analyses are available, then no prioritization of names should be decided. It will be a task of each expert committee's members to draft proposals of preferred names and vote on them. For example, *Hypocrea* vs. *Trichoderma* is being debated within the International Subcommission on *Trichoderma* and *Hypocrea* Taxonomy (ISTH); its outcome will be reported to the ICTF and NCF, who may (or may not) confirm it and publish their decision. In this case, the cellulase producer *Trichoderma reesei* and some other biocontrol strains of *Trichoderma* spp. are commercially important. Although the name of the *T. reesei* correlated teleomorph, *Hypocrea jecorina*, is also becoming widely used, preference would be given to *Trichoderma*, which is the older name anyhow. Does a preference for *Trichoderma* then force species

like *H. pulvinata* (in the anamorphically little-differentiated *Trichoderma* sect. *Hypocreanum*) and *H. danica*, *H. peltata*, *H. rhododendri*, *H. spinulosa*, etc. (no anamorphs) (Jaklitsch 2011) into *Trichoderma?*

The problem is that there are a) several groups of fungal taxa on which nobody is really working and b) other groups that are being well studied but by different authors with entirely incompatible concepts. How can a committee scenario work in these cases?

The implication that "expert groups" shall join in committees to treat their respective fields of specialty may pose serious problems. Taxonomic concepts in the *Eumycota* have always been highly variable (including even the name for all fungi). The introduction of molecular phylogenies raised the hope that such controversies might be resolved, but we now know this will not be the case. In fact, progress with molecular phylogenetic studies for diverse higher fungal taxa has been highly variable and depends on the variably patchy funding available to taxonomic specialists in different fungal groups. Sound molecular phylogenies are very difficult to achieve for innumerable fungal taxa for which most constituent species are neither epitypified nor available in cultures. Many who supported implementation of the 1F=1N concept seem not to have realized that morphological and other phenotypic data still provide more information on which to base classifications, especially where a limited number of sequenced genes fails to provide convincing proof of relatedness.

It is gravely worrying that TOO MANY new layers of authorities whose opinions may differ (and, indeed, be mutable) are injected into what was previously a process with universally recognized rules based on priority and an established line of authority to achieve stable, enduring nomenclatural decisions. The new system of committees adjudicating names EN MASSE means that research findings not favored by a committee can simply (and dangerously) be "voted out" of official recognition.

Suggested general working rules for committees

Names of genera

Anamorph and teleomorph genera were hitherto based on anamorph and teleomorph traits, respectively. Adoption of unitary nomenclature necessitates emending all pleomorphic generic diagnoses to recognize both anamorphic and teleomorphic characters, whether present or not. All mycologists should welcome such improvements because separating information about alternate morphs into multiple descriptions fails to communicate vital and complete information about the whole organism. Although we have often recognized some degree of polyphyly in many important anamorphic genera, we have until now preferred that teleomorphic genera be (as far as possible) monophyletic. The inverse situation may arise, however, when a more narrowly defined

anamorphic genus takes precedence over a teleomorphic one. In that case, the teleomorph genus may continue to be used as an artificial "dustbin" of teleomorph species with or without known anamorphs. For example, many *Mycosphaerella* anamorphs may be submerged into some morphologically and phylogenetically well-defined anamorphic genera such as *Cercospora* and *Ramularia* (Crous et al. 2009, Crous 2010), thus forcing *Mycosphaerella* to become a "dustbin" for species without known anamorphs. An equally undesirable alternative would be combining many hundreds of species from several anamorph genera into *Mycosphaerella*, which already contains ca. 2000 species. Morphological comparisons among species would become impossible in such a huge genus unless anamorph characters were correlated with phylogenetic ones. To avoid such problems, will we be forced to accept gigantic genera characterized only by statistics based on (minimal) DNA data?

If *Puccinia* were prioritized over *Uredo* s.str., the synonym *'Uredo'* would not be available for species with different teleomorphs, thus requiring the proposal of new generic names to accommodate them. Art. 14.13 may need to be amended in order to repair this undesirable situation.

Serious problems will arise for teleomorph genera such as *Cordyceps* and its recent segregates, each of which is associated with multiple distinct anamorph genera — many of which may form distinct clades and have names with nomenclatural priority over their linked teleomorph genus. Further splitting of (teleomorphic) genera may become advisable in such cases rather than lumping multiple disparate anamorphs within one teleomorphic genus.

This situation is exemplified by the relatively rare Asian teleomorphic genus *Metacordyceps* G.H. Sung et al. (*Hypocreales*: *Clavicipitaceae*) (Sung et al. 2007; also see Kepler et al. 2012) whose anamorphs include the globally distributed, commercially important entomopathogenic genera *Metarhizium* Sorokīn 1883 and *Nomuraea* Maubl. 1903, as well as *Pochonia* Bat. & O.M. Fonseca 1965 (including species used for biocontrol of nematodes) and other species not placed in any anamorphic genus after the phylogenetic reclassification of *Paecilomyces* sect. *Isarioidea* Samson 1974 (Luangsa-ard et al. 2005, Sung et al. 2007). That these anamorph genera are phylogenetically and ecologically distinct may justify the preferential use of the anamorph names. Nevertheless, the younger teleomorph name *Metacordyceps* also carries relevant information. Although we generally prefer to retain precedence for the teleomorph-typified generic name over its correlated anamorphic name, we must accept exceptions.

Exceptions to the precedence of teleomorph-generic names

Exceptions from this rule are allowed, although objective criteria are not yet clearly worded in the new Art. 57.2. To the *Trichoderma-Hypocrea* and *Metarhizium-Metacordyceps* examples noted above, we add the so-called

"macromycete" groups (those forming conspicuous stromata) in *Ascomycota* for possible exception.

Some *Hypocreales* (as in other ascomycete groups with economically important species, such as plant parasites or industrially cultivated fungi) have already been studied thoroughly by molecular methods. Taxonomic authorities familiar with these fungi will tend to follow the molecular results to adjudicate the status of the core taxa. However, their anamorph names for some of these fungi may prevail in future nomenclature, because the anamorphic stages that cause the conspicuous disease symptoms were described long before their corresponding teleomorphs. Nonetheless, nearly all xylarialean experts will admit that the number of taxa whose molecular characters have already been thoroughly evaluated is wholly insufficient to make final nomenclatural determinations, since the phylogenies based on housekeeping genes vs. rDNA present wholly divergent results about relationships among these fungi. The numerous experts (all also signatories of Gams et al. 2011) will surely agree that there is no need to change the current taxonomic system. Anamorphs of *Xylariales* are widely known but treated as synapomorphies, so that dual nomenclature was abandoned for these genera decades ago, whereas such well-known and conserved generic names as *Xylaria*, *Hypoxylon,* and *Daldinia* continue to take preference. Their anamorphic names are actually used as features that characterize subfamilies (or, in the future, perhaps, families or orders). The so far prevailing preference for teleomorph names could or should be adapted for all *Ascomycota* unless very serious reasons (including priority) make it more practical to adopt the anamorph name (as for *Penicillium* and anamorphs of *Metacordyceps*).

The latest revision of *Penicillium* (Samson et al. 2011) provides more examples: the teleomorphic name *Eupenicillium* has had little application or relevance, with *Penicillium* already treated as holomorphic by Raper & Thom (1948); however, for species of the more distantly related teleomorphic *Talaromyces* (whose anamorphs in *Penicillium* sect. *Biverticillium* still needed a new generic name), the teleomorph name was chosen to replace the better known anamorphic names in *Penicillium*. Must all these cases be decided again in the newly prescribed High Courts of Mycology by jurors yet to be selected?

In the future, teachers of mycology may be hard pressed to explain to their students why some genera of the *Xylariaceae* have nodulisporium-like or geniculosporium-like anamorphs but those of the "*Trichodermataceae*" (or "*Trichodermatales*") have *Hypocrea*-like teleomorphs. Recruitment of young fungal taxonomists is already very difficult; those who led the 1F=1N movement and championed the decisions adopted in Melbourne even used this difficulty as a major argument in their favor. Teaching of mycology MIGHT become more complex if suprageneric taxonomic ranks were often based on anamorphic

names, but such an argument seems to give little credit to the ability of students to understand these complications.

A further consequence of complex connections between anamorph and teleomorph genera is the necessary recognition of **paraphyletic genera,** such as *Lecanicillium*, which Gams & Zare (2001) described, at the same time recognizing its paraphyly. The current PCR-driven, monophyletic world view also seems to reject the perfectly valid, widely held position that paraphyletic taxa are not only acceptable, but that recognizing them as such is natural and appropriate. Zoologists, who have long accepted the reptiles as a transitional group from which the birds have arisen, do not deny *Reptilia* its own taxonomic status, even where both molecular and comparative anatomic studies prove that birds + reptiles are a paraphyletic class. It is hard to grasp why some mycologists fervently want to impose strict monophyly on all fungal taxa even where gene-based data supporting such a conclusion are unavailable or may be unobtainable) (Hörandl & Stuessy 2010).

When a new teleomorph is discovered for a known anamorph, it will no longer be possible to describe it in a new genus unless that species is proven phylogenetically not to be congeneric with the type of the anamorph genus.

If the type species of a genus has not been studied by gene-based methods, the genetic homogeneity of the genus cannot be proven. Similarly, no unification of anamorphs and teleomorphs can be forced if the type species of both the anamorph and teleomorph genera have not been analysed.

Names of species

If the rule of priority were strictly applied to epithets in both teleomorphic and anamorphic genera, many name changes would ensue unless a particular, well-established name is 'rescued' by formal conservation. To avoid this, we suggest a procedural rule for the committees (probably eventually for a new article in the Code) that binomials established before July 31, 2011 for either morph type must not be replaced by combining older epithets available in the 'opposite' morph (e.g., *Trichoderma reesei* should not become '*T. jecorinum*' and *T. citrinoviride* should not become '*T. schweinitzii*' despite the older available name *Hypocrea schweinitzii*). If *Pleospora* were retained over *Stemphylium*, would the new combination '*Pleospora botryosa*' then have to replace the established but younger *P. tarda*? In parallel with the ICBN Art. 11.2, such a rule would stipulate that priority applies only to names of the same rank or the same prioritized genus.

Another problem concerns species for which no sequence data are available. Can they be recombined into the alternative morph's genus or not? Would they remain in limbo? After proving the linkage of the type species of both anamorph and teleomorph genera, it would be better to combine all other names from the suppressed genus into the prioritized genus to keep them

visible and usable, even if those types were never restudied by any means. If not, they will be forgotten, any further revisions of them would halt, and homonyms or synonyms might be created in the prioritized genus.

Such issues are further complicated because innumerable older (and many highly important) species were not typified when described or their type specimens are lost; these taxa would require lecto-, neo-, and/or epitypifications before drawing any gene-based taxonomic conclusions about their status. The problems raised by so many fungi that were described from single collections and that may be extremely rare or difficult to re-collect again for DNA-based studies are nothing less than a daunting impediment for the establishment of a workable 1F=1N taxonomy.

Conclusions

A major aim of the one-fungus one-name policy was to simplify fungal nomenclature. The question, however, remains: simplification for whom? For the convenience of present-day mycologists, it would be desirable not to change the names of higher taxa. When in extreme cases an anamorph-generic name replaces the type genus of teleomorph-based higher taxa (e.g., *Hypocreales*, *Hypocreaceae*), we still remember the meaning of the higher taxon because we are used to it. The situation becomes complicated for future generations, however, who must deal with many previously teleomorph-based higher taxa when the teleomorph genus is no longer in use; mycologists must then learn that these names were based on a now-rejected nomenclatural practice and try to understand the superseded taxonomies BEFORE they can apply the systematic concepts that led to the current use of a name. The intended "simplification" imposed by the 1F=1N standard will thus not be achieved in a long-term vision, and future mycologists will still need to understand the suppressed dual nomenclature to deal with the historical literature. Moreover, many recently introduced teleomorph-generic names do reflect improved phylogenetic knowledge, although they will not successfully compete with the correlated anamorph names; these names undoubtedly will retain their informative value in naming clades and should not, therefore, be completely eliminated.

In a carefully balanced system of prioritization, future mycologists may appreciate having the choice between either continuing to use the present higher-rank taxon names or creating new anamorph-based names.

An essential, permanent remnant of the dual nomenclature will be the need for listing all teleomorphic and anamorphic synonyms of a fungus in any monographic treatment together with the typifications of all these names. It will often be the case that more species were described under the suppressed morph-generic name than in the officially recognized morph genus. In any case, all these suppressed species will have to be re-studied before any new species can

be described. This does not simplify future taxonomic work. Re-examination of types must be possible any time, and this will involve morphological (including ultrastructural), biochemical, and molecular approaches equally, all still subject to improvement. Curiously, it is often more valuable to preserve teleomorphic material of most ascomycetes in a herbarium than their anamorph which, if the type is a dried agar culture, can display its properties only when reactivated in culture.

In a unified nomenclature, fungi will continue to have complicated life cycles displaying a teleomorph and one or more anamorphs, each with its distinctive gene expression and biological and ecological role. Future students of mycology will have to understand the concept of anamorph and teleomorph to understand the biology of the fungus, even if all stages are encompassed under a single name.

The first paragraph of the Preamble of the ICBN contains an odd and ominously predictive stipulation immediately before the sentence quoted above: "The purpose of giving a name to a taxonomic group is **not to indicate its characters or history** [our emphasis added], but to supply a means of referring to it and to indicate its taxonomic rank." It seems probable that few mycologists who deal with pleomorphic fungi would appreciate the strict application of such a stipulation. The nomenclaturally required consolidation of many morphologically disparate teleomorphic and anamorphic forms and even genera into single genera now required by the newly adopted standard of 1F=1N may satisfy both the new Code and advocates of strict monophyleticism but this process will create many significantly large and diverse — but nomenclaturally supported! — genera that will also be self-accreting mycological 'black holes'. The names of such 'megataxa' will bear no useful biological information about their species. While this result will conform with the newly redefined (if artificial) sense of nomenclatural stability, it cannot be hailed as progress toward biological or even taxonomic sensibility.

We should also note that the availability of cultures of hitherto unknown fungal organisms is an absolute prerequisite for their future exploitation in biotechnological applications. Fungi have historically been used for many beneficial purposes; curiously, the roots for the new concepts and changes adopted in Melbourne seem to have been elaborated mainly for organisms that were studied intensively for their diverse beneficial or detrimental properties — e.g., pathogenicity, production of mycotoxins or other primary or secondary gene products, uses as biological control agents, or many other potential concerns. We should realize that in view of future applications, we have so far only dealt with the low-hanging fruits. Large-scale bioprospecting programs are now under way, and potential uses for fungi are by no means restricted to the traditional search for novel, badly needed antibiotics and other compounds

with potential utility in pharmaceutical or agrochemical indications. The search for industrial enzymes and commodity chemicals for "White Biotechnology", as well as renewable resources (biofuel production), bioremediation, etc., will almost certainly become more important in the future. Innovative methods of genomics research will allow for the exploitation of slow-growing organisms, e.g., by transfer of their genes into heterologous hosts where biotechnological applications appear feasible.

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